Brief reports

The onset of incubation and hatching asynchrony in the Barn Swallow *Hirundo rustica*

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Introduction

Current literature is inconsistent concerning the exact time when female Barn Swallows *Hirundo rustica* start incubation and the degree of hatching asynchrony in this species. Cramp (1988) states that they begin incubation with the last egg in the clutch and that hatching is synchronous. Ehrlich et al. (1994) also characterize the Swallow as a synchronously hatching species. Møller (1994) says that the start of incubation in his study population is after the penultimate or ultimate egg is laid and that broods hatch over one to three days. On the other hand, Turner (1994) [p.81] claims that "incubation does not start in earnest (...) until the last egg is in the nest". Her description implies that differences in hatching time result from the warming of eggs by females spending some time at the nest, especially at night. In this paper we present some preliminary results showing that incubation in the majority of cases started before clutch completion, with hatching asynchrony being a result.

Methods

We started studying the biology of swallows nesting at a big farm in Goślub, central Poland (52°05'N; 19°28'E), in the spring of 1994. Forty nests, 20 first broods and 20 repeated and second broods, were controlled every day during the laying and hatching periods and at least once a week otherwise. Both the pattern of incubation and the order of hatching were observed in 16 clutches, so that the relation between these two processes could be exactly studied. In the remaining cases, the pattern of synchrony/asynchrony was inferred from the time spread of hatching, which is a frequently applied practice in analogous studies (Magrath 1990; Harper et al. 1993).

Noticing the precise moment of the start of incubation is difficult because females can sit on the nest, without incubating the eggs (Turner 1994). However, after they initiate incubation, the females spend most of the day sitting on the eggs, except for short periods when they leave the nest. We observed five selected nests for three to four 15–30 minute periods a day, mostly in the morning and early afternoon, during the time of laying eggs (6–7 days), so that the total time of observation of particular nests ranged from 6 to 9.5 hours. Although we did not measure it precisely, we *ex post* assess that incubating females spent at least two-thirds of the day on the eggs. We also observed a behavioural shift in incubating females. After starting incubation they become less timid, and it is sometimes difficult to make them get off the nest. Moreover, incubated eggs are clearly warm whenever touched. Consequently, we classified clutches as incubated by combining the above criteria. The nestlings were measured (wing length) and weighed two to three times during the nestling period. It was possible to assess age differences among nestlings on the basis of their wing length and qualitative age-dependent traits like egg tooth, blindness, opening the eyes, and the development of feathers (Lyuleeva 1974, McGinn & Clark 1978, Koloyartzev 1989, Zieliński 1993). Adult birds were also trapped at the nest sites with mist nets. They were ringed, measured and released (for details of the same procedure, see Bańbura (1986)).

Results

Hatching was considered synchronous when all nestlings at a given nest appeared within one day, and asynchronous when nestlings were observed to be hatching throughout a period longer than 24 h. Among the 16 clutches observed in detail, three clutches, whose incubation started after the last egg was laid, hatched synchronously. In the remaining 13 clutches incubation began with the penultimate eggs or with the second egg from the last one. In these clutches hatching occured asynchronously, with the hatching spread consistent with that expected from the incubation pattern.

Most broods were characterized by an early beginning of incubation and asynchronous hatching. The proportion of first broods which hatched asynchronously was 0.85 ± 0.082 (SE) (N = 20), and the analogous value for second and repeated broods pooled was very close to the former, 0.80 ± 0.092 (SE) (N = 20). The proportions of synchronous and asynchronous broods did not differ between these two brood categories (G = 0.174, df = 1, NS).

The proportion of clutches hatching synchronously was relatively high among two to three egg clutches, 0.57 ± 0.202 (SE) (N = 7), whereas it was only 0.09 ± 0.051 (SE) (N = 33) for four to six egg clutches. This relation is significant for all clutches pooled (2-tailed Fisher's exact test: P = 0.022, N = 40). However, it is not a perfect relation, as a two egg asynchronous clutch and a five egg synchronous clutch were observed.

Discussion

The prevailing belief that European Barn Swallows not only start incubation after completing laying eggs, but also the eggs hatch synchronously (Cramp 1988) is perhaps incorrect as a generalization. Many authors recorded a hatching spread of one to two days in different populations (e.g. Adams 1957, Kuźniak 1967, Georg & Al-Rawy 1970, McGinn & Clark 1978, Ribaut 1982), and von Haartman (1969) pointed out that this may result from incubation commencing before the clutch was complete. We are not aware of any population where synchronous hatching or incubation starting after clutch completion prevails. McGinn and Clark (1978) suggested that nestlings hatch in the order of egg laying, however, they did not investigate the relative time from the beginning of incubation. In this study we observed some females starting incubation with the second egg from the last one as well as many more of them beginning incubation with the penultimate egg. We think that such early initiation of incubation is the true reason for asynchronous hatching rather than occasional short-term brooding as suggested by Turner (1994).

It is interesting that in American populations of the Barn Swallow (*Hirundo rustica erythrogaster*) the degree of hatching asynchrony resulting from early incubation seems to be higher than in Europe (Samuel 1971). This may be connected with biparental brooding, which is characteristic of American swallows (Nilsson 1993).

It is worth noting that within-population, and perhaps between-population, variability exists for the time when females start incubation and, as a consequence, in the extent of hatching asynchrony. This variability seems to be connected to some extent with clutch size, but other variables are probably also involved. The relation with clutch size is especially interesting in the context of the egg-viability hypothesis of hatching asynchrony (Arnold et al. 1987, Veiga 1992). This hypothesis suggests that incubation is initiated before clutch completion because the unincubated egg mortality rate increases with time due to over-cooling. The fact that among the analysed clutches five first eggs, but only two second, two fifth and two sixth eggs failed to hatch seems also to be in agreement with this hypothesis.

Our data set is too small to test adaptive hypotheses of hatching asynchrony (Magrath 1990). Although, it seems possible that the degree of hatching asynchrony in swallows can facilitate brood reduction, we did not find any evidence for it at this stage of our study; the same proportion of brood reduction occurred in synchronous (1 out of 6) and asynchronous broods (5 out of 32) (G = 0.004, df = 1, NS). Hatching asynchrony is the main source of nestling body-size variation and perhaps competitive abilities, as there is no clear pattern of egg-size variation related to laying sequence (Bańbura & Zieliński 1995).

The causes and consequences of the various degrees of hatching asynchrony observed in the swallow would certainly be worth studying further. Detailed information on the extent to which clutches of different completeness are incubated and the average incubation temperature would be desirable.

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